Table 2 Kerogen typing

Phytoplankton	4.5%	Total marine derived 51.5%
Amorphous kerogen	47%	
Wood	31%	
Cuticle	2.5%	Total terrestrial derived 48.5%
Spores/pollen	15%	

'upland' flora. The presence of acritarchs and dinocysts, well known from the nearby Rhaetian sections, indicate a marine input into the fissure. By analogy with the findings of Wall in some British Jurassic strata[12], the occurrence of the acritarch *Michystridium* sp. (as opposed to *Veryhacium*) suggests a near-shore (brackish?) environment and explains the absence of a stenohaline marine fauna. A morphological typing (Table 2) of the total kerogen shows that nearly half is amorphous organic material. Amorphous organic material is usually considered to have formed diagenetically[13] in marine conditions from algal biopolymers, through a monomer stage to give a condensed geopolymer. The high proportion of amorphous organic material in combination with the consanguineous Rhaetian dinocysts indicate a strong marine component and preclude any suggestion that the marine input was blown into an upland fissure by surface winds.

We postulate that the fissure was partly submerged under the transgressing Rhaetian sea. There is a patch of 'Rhaetic' (probably of the upper Westbury Beds) exposed 1 km south of the quarry and at a present-day altitude of over 20 m above the fossil-bearing cavern. This strengthens the suggestion that the lower fissure levels were flooded by saline waters; these would have brought in the organic-walled phytoplankton and provided the precursors for the formation of the amorphous organic material. At the same time, terrestrial vertebrates living around the entrance of the fissure and land-derived sporomorphs (showing no anomalous 'upland' elements) either fell or were washed into the cavern and were deposited with the marine palynomorphs.

This reconstruction of the environment exposes the anomaly of well preserved late Triassic 'upland' reptiles in a marginal marine deposit. Also, in the past, the difficulty of accurately dating 'upland' reptiles has meant that some 'lowland' taxa used for the comparison may not have been contemporaneous (for example, the last known record of a rhynchosaur is mid-Norian[14] whereas the Tytherington upland reptiles are Rhaetian). In view of these findings we suggest that the loose term 'upland' cannot prudently be applied to distinguish these fissure reptiles from those of other late Triassic sediments.

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The first fossil cephalopod statoliths to be described from Europe

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Statoliths of cephalopods are small, hard calcareous stones which lie within the cartilaginous skulls of octopods, sepioids and teuthoids[1]. Fossil statoliths, clearly belonging to genera which are alive today, have previously been described from 11 Cenozoic deposits spanning from the Eocene to the Pleistocene in North America[2–5]. Such statoliths are of particular interest because they provide a means of studying the evolution of living cephalopod groups which have no calcareous shells, including the cosmopolitan and numerous teuthoids and octopods. Here, the first cephalopod statoliths to be recognized in European deposits are described and identified as *Loligo* sp. They are compared with the North American fossil *Loligo* species and statoliths removed from the two living *Loligo* species of Europe.

Cephalopod statoliths were found in two Burdigalian outcrops of the Southern Aquitanian Basin (early Miocene: age 20–16 Myr). Blue-greyish fine sand was sampled at the hamlets of Paillon, Poyartin (French geological map 1/50.000; XIV–43, Dax: coordinates $x = 342.100$, $y = 158.420$) and Jean Tic, Saubrigues (XIII–43, Saint-Vincent-de-Tyrosse: coordinates $x = 305.550$, $y = 152.050$), and each sample of 750 kg only yielded three statoliths. The deposits occurring at Paillon are considered to be synchronous with the Burdigalian stratotype deposits of northern Aquitaine, whereas those from Jean Tic,

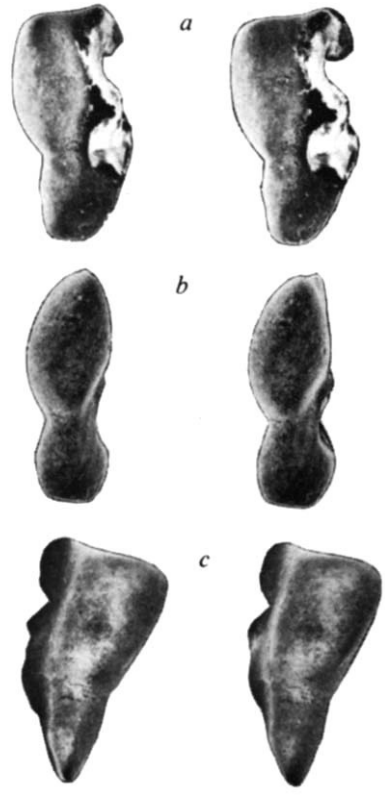

Fig. 1 *a–c*, Three stereo pairs of a fossil *Loligo* statolith (BM(NH) No. C46952) from a Miocene deposit in Europe photographed with a scanning electron microscope. These should be copied and suitably separated for obtaining a three-dimensional effect with a stereo viewer. Length of statolith = 1.75 m.

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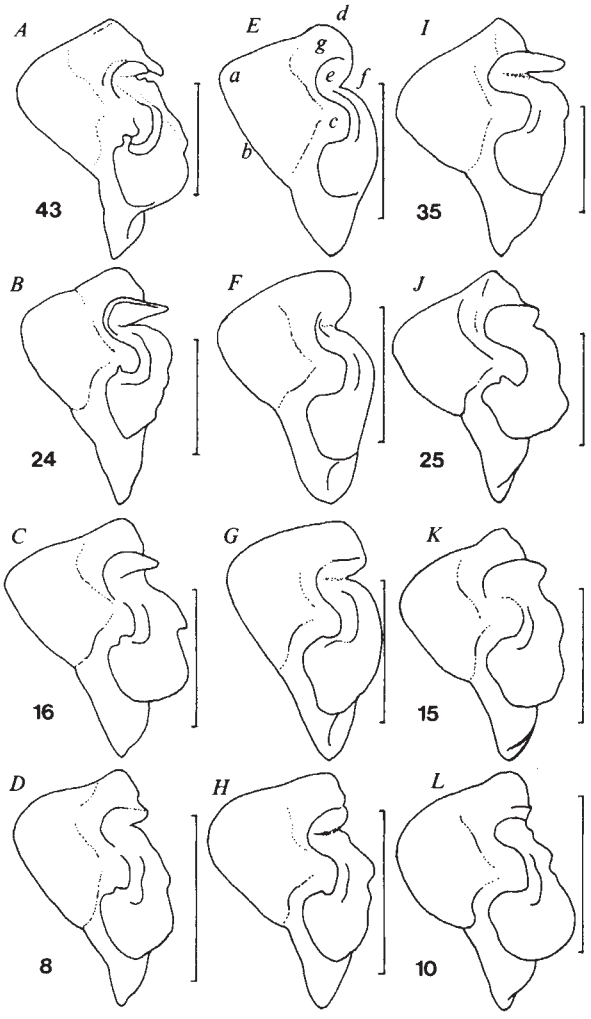

Fig. 2 Anterior views of *Loligo* statoliths. *A–D, L. vulgaris*; *E–H*, Miocene fossil statoliths from Europe (BM(NH) Nos. C46953–6). *I–L, L. forbesi.* Statoliths are shown as the same length to emphasize variation in form. Scales indicate 1 mm. The dorsal mantle length of the squids from which the statoliths were removed are indicated to the nearest centimetre. Drawings of statoliths *F–H* were reversed because they were the opposite side (left) to the others. Note that *E* and *F* are nearly the same length as *C*, *G* and *K*.

generally known as 'the Marls of Saubrigues', are certainly younger (? Upper or Post Burdigalian) and formed at greater depths[6].

The overall shape of these six statoliths is closely similar to statoliths removed from living *Loligo* species and clearly different from statoliths of cephalopods in other families. In particular, the lateral dome is broadest and rather pointed at its dorsal end (Figs 1, 2*a*), the lateral dome is not divided into superior and inferior lobes (Fig. 2*b*) and is oval from the lateral side and the spur is prominent and almost square (Fig. 2*c*). Other notable features are that the dorsal dome extends dorsally further than the lateral dome (Fig. 2*d*), the dorsal indentation (Fig. 2*e*) is smaller than the ventral indentation being both shorter and narrower, there is a distinct medial fissure (Fig. 2*f*) and the anterior surface of the dorsal dome is flat but not markedly deflected anteriorly (Fig. 2*g*). Although previous work shows that certain of these features distinguish between several *Loligo* species examined elsewhere and statolith shape varies between individuals and with growth (Fig. 2), when these variations are taken into account there are no other obvious features which distinguish between the fossil and the two living species of Europe *Loligo vulgaris* Lamarck 1799 and *Loligo forbesi* Steenstrup 1856. The North American fossil species are more easily distinguished from each other[3].

Comparison of these European fossils with North American fossil species shows that the European are closest in general shape to *Loligo mississippiensis* Clarke & Fitch 1979 from the Lower–Middle Oligocene deposit at Vicksburg, Mississippi[3]. They differ, however, from this species in having a less sharply pointed lateral dome which is more rounded anteriorly and ventro-laterally and has a deeper medial fissure.

To examine the species relationships further, nine dimensions of all the statoliths were used in a multiple discriminant analysis[4]. The measurements were defined previously[1,3,4] and are termed total length (tl), rostral length (rl), lateral dome length (ld), ventro-lateral length (vl), dorso-lateral length (dl), dorsal dome length (dd), dorsal-tip-to-spur length (dts), maximum width (w) and thickness (th). This analysis maximizes the differences between the species on the basis of combining all nine dimensions and extracting axes in decreasing order of importance. Thus, the first and second axes used here account for the greatest proportion of the total variance and give the best separation between the species.

The six European fossil statoliths fall into two size groups of three, corresponding to the two sites from which they were collected, and as the *L. vulgaris* and *L. forbesi* statoliths also both fall into two such size groups the analysis was run with nine groups, six for these three species and three American fossil species. The first two axes extracted accounted for 94% of the total variation between groups and were both significant at $P = 0.001$. All the scores on these two axes were standardized and the means and standard deviations of each of the nine groups are plotted (Fig. 3*A*).

Although there was some variation in the standard deviations between groups, the dispersions of the original variance–covariance matrices were not so different as to invalidate the discriminant analysis. The direction and magnitude of the effect

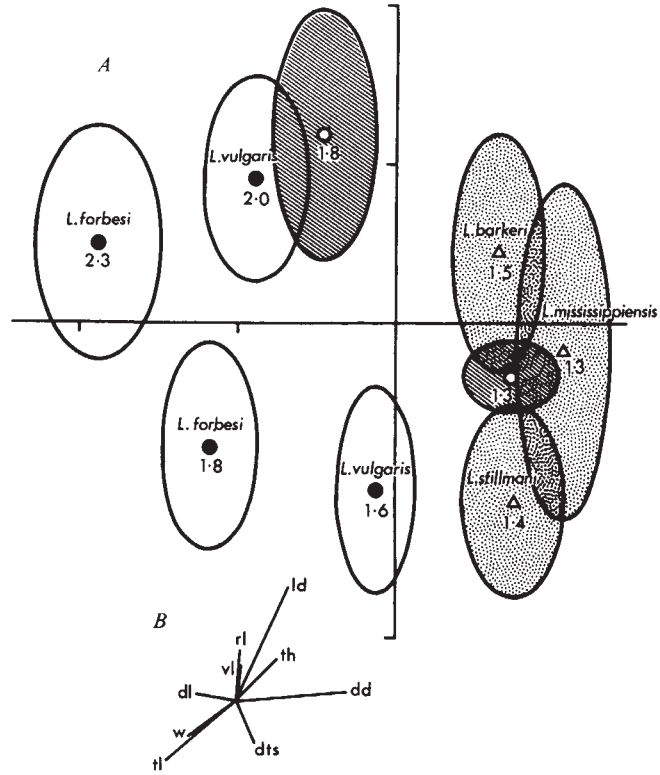

Fig. 3 *A*, Results of the multiple discriminant analysis of statoliths of three North American fossil species (stipled), one European fossil species (hatched) and two European living species of *Loligo*. The mean position of each species (or group) is plotted on the first two discriminant axes, with ellipses representing 1 s.d. for each group on each axis. The mean total length (in mm) of statoliths is given for each group. *B*, The relative weightings of the nine measurements on the axes. The measurements are identified as described in the text.

of each of the nine measurements on the separation of the species on the two axes are shown in Fig. 3*B*.

The spatial relationships between the groups of large and small statoliths of *L. forbesi*, *L. vulgaris* and the European fossil are very similar despite the fact that the fossil statoliths are smallest. This may suggest that the fossil species grew to a smaller adult than the living species. These fossils are approximately the same size as statoliths from *L. forbesi* and *L. vulgaris* individuals, with dorsal mantle lengths of 8.3–15.8 cm (Fig. 2). As the size of statoliths in the Loliginidae is closely correlated with the dorsal mantle length of the animals[5] it is likely that the fossil statoliths came from animals having mantle lengths of approximately 8–16 cm.

When the scores for all individual statoliths were plotted on the first two axes there was no overlap between *L. forbesi* and any of the fossils, whereas the larger *L. vulgaris* overlapped with the larger European fossils. The smaller *L. vulgaris* overlapped with *Loligo barkeri* and *Loligo stillmani* and the smaller European fossils overlapped with all three American fossils.

Thus, although differences between the species are rather too subtle to make identification possible between individual statoliths of *L. forbesi* and *L. vulgaris* or *L. vulgaris* and the large European fossils, discriminant analysis shows that there is a definite trend in form from the American fossils through the European Miocene fossil and *L. vulgaris* to *L. forbesi* (Fig. 3). Although the difference between the two size groups of the European fossil shown in Fig. 3 is probably a function of size, it might indicate a difference in species, because they come from different sites whose fauna show some differences. For example, the fish otoliths assemblage of Paillon, in which the smallest statoliths were found, differs from that of Jean Tic in having no mesopelagic representatives and in having many genera which are restricted today to the Indian Ocean. In addition, the association of Jean Tic contains some typical species recorded only from younger strata (ref. 6 and unpublished data). Such features are due to the difference in depth of deposition, but also reflect slight differences in age.

These data show that *L. vulgaris* or a closely similar species lived in European seas during the early Miocene. These seas were rather shallow (~30 m; the deepest parts, the canyon in which the Marls of Saubrigues were deposited, certainly did not exceed 300 m) and the climatic conditions were similar to those on the Atlantic coast of southern Morocco today.

Thus, the form of the statolith has remained virtually unchanged during a period of 20 Myr.

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Best shape for nature reserves

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The ideas of classical island biogeography[1] have been used[2–6] to derive rules for the optimal design strategy for nature reserves. For example, Diamond[3] states that, given limited (financial) resources, it is better to purchase a few large reserves rather than many small ones of equal total area; and that reserves should be as close to one another as possible. The validity of some of these rules has, however, been questioned[7–10]; for example it has recently been shown[9,10] that several small reserves may contain more species than a single one of equivalent area. These rules have nevertheless been accepted uncritically by others, including the IUCN[11]. Here, I examine Diamond's rule[3] that reserves should be as round as possible and conclude that in certain circumstances the optimal shape may be other than circular. There is no *a priori* reason for believing that these circumstances are unrealistic, and I know of no observational evidence to suggest whether they are found in nature or not. I also reason that the rule that reserves should be as close to each other as possible is inconsistent with the statement that they should be circular.

According to the tenets of island biogeography, the number of species inhabiting islands or isolated habitat patches (such as many nature reserves) is governed by the rates of extinction and immigration[1]; when these balance each other on average, the number of species is in equilibrium. If the extinction rate is higher than that of immigration, the island is supersaturated and the number of species will decline or 'relax' towards equilibrium. The rate of relaxation or net loss of species can be reduced by decreasing the rate of extinction or by increasing that of immigration and the purpose of Diamond's rules is to achieve both of these. For example, he states[3] that a large reserve is preferred to a smaller one because, amongst other things, it will have a lower extinction rate; and that reserves should be "as close to each other as possible . . . to increase the immigration rates between reserves".

If immigration into nature reserves is indeed an important factor maintaining the total number of species, then it is questionable whether reserves should preferably be circular as this requirement implies the reduction of extinctions without reference to any simultaneous effects on immigration rate. To many dispersing organisms the apparent size of an island, and therefore the probability of colonization, must be more a reflection of the island's linear dimensions perpendicular to the direction of travel, that is the apparent width and height, rather than the area (J. L. Harper, personal communication). Therefore, immigration rate will depend on shape, not just area, whether the organisms are dispersed by voluntary or involuntary means. Thus, whereas departure from circularity may adversely affect extinction rate, this may be ameliorated by an increase in the immigrant population. The optimal shape for a reserve will depend on the balance between these two factors.

To investigate this quantitatively, define the dimensionless parameter R by[12]

$$R = \frac{p}{2(\pi A)^{1/2}}$$

where p is the island perimeter and A its area. R is a simple measure of shape; for any given area A, R may vary from unity for a circular shape to infinity for an infinitely long and narrow one. R is 1.1 for a square and 5.7 for a hedge 100 m long by 1m wide; the greater the departure from circularity, the greater is R.

Assuming that the effects of shape act independently of other influences, such as area and isolation, the average extinction and immigration rates, E and I, may be approximated by[1,4,13]

$$E = SVf(R)$$

$$I = (P - S)Ug(R)$$

where $f(R)$ and $g(R)$ are functions describing the effects of shape on E and I, S is the number of species present on the island at the given time, P is the total number of species in the species pool available for colonization, and V and U express the effects of other factors such as area, isolation, habitat diversity and such. To simplify the analysis, I ask: what value of R maximizes the equilibrium number of species, S_0? An alternative but qualitatively similar question would have been: what

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